Cheilostome bryozoans from the Upper Cretaceous of the Drumheller area, Alberta, Canada

PAUL D. TAYLOR

Department of Palaeontology, British Museum (Natural History), Cromwell Road, London SW7 5BD

ROGER J. CUFFEY

Department of Geosciences, Pennsylvania State University, University Park, Pennsylvania 16802, U.S.A.

SYNOPSIS. As part of a systematic revision of the relatively scarce Cretaceous bryozoan faunas of the North American Western Interior, two encrusting cheilostome species from the lower Maastrichtian part of the Edmonton Group near Drumheller in Alberta are here revised. *Conopeum bicystosum* Allan & Sanderson, 1945 is designated the type species of the new genus *Eokotosokum*, a 'malacostegan' characterized by zooids with well-developed cryptocysts and two large distal spine bases. A second species, *Wilbertopora? lintonensis* Cuffey, Feldmann & Pohlable, 1981, originally described from the Fox Hills Sandstone of North Dakota, is assigned to *Villicharixa* Gordon, 1989, on account of the numerous small spine bases which are obscured by a ferruginous crust in the holotype specimen. Both *Eokotosokum bicystosum* and *Villicharixa lintonensis* lack ovicells and are inferred to have possessed planktotrophic cyphonautes larvae, in contrast to the majority of contemporaneous European species which had ovicells and non-planktotrophic larvae. They probably inhabited a brackish estuarine environment. Reasons for the depauperate bryozoan fauna of the Western Interior Cretaceous Seaway are discussed in brief.

INTRODUCTION

In spite of extensive searching and collecting, few bryozoans have been encountered in the Cretaceous of the Western Interior of North America. Their scarcity is sufficiently striking, especially in comparison with western Europe (e.g. Voigt, 1979, 1981, 1983), to require explanation. Although a few possibilities are suggested below, the systematics of the bryozoans present in the Western Interior must be re-evaluated on a consistent comparative basis before palaeo-biologically reasonable possibilities can be fully explored. The purpose of this paper is to describe one of the most abundant bryozoan occurrences in the region.

Conopeum bicystosum Allan & Sanderson, 1945, was originally described from the Edmonton Group of central Alberta on the basis of very limited material. More extensive collections from Alberta confirm that this species greatly dominates the Maastrichtian bryozoan fauna of the Edmonton Group but requires re-assignment to a new genus, *Eokotosokum* (p. 17). One specimen, however, belongs to a different species, *Wilbertopora? lintonensis* Cuffey, Feldmann & Pohlable, 1981, originally described from an approximately correlative horizon in North Dakota, and here re-assigned to *Villicharixa* Gordon, 1989.

The results of the present study fall into the same pattern as was suggested by a preliminary survey of the Western Interior Cretaceous bryozoan literature (R.J. Cuffey, unpublished), namely a small number of distinctive species, which are difficult to assign generically, occur. This may imply the occasional establishment of local endemic populations, scattered geographically and geochronologically up and down the Western Interior Cretaceous seaway. The region's bryozoan fauna thus contrasts markedly with the more diverse and abundant bryozoans evolving contemporaneously in Europe. Explanations for this contrast have tended to focus upon the inferred harsh or stressful conditions which may have prevailed within the seaway, such as lack of suitable substrates on its extensive soft 'soupy' bottoms, and extreme fluctuations in salinity or dissolved oxygen concentration beyond the tolerance limits within which most bryozoans could survive (Fig. 1) (Frey, 1972; Hattin, 1975, 1982; Kauffman, 1975, 1986; Bottjer *et al.*, 1978; Arthur & Schlanger, 1979; Arthur *et al.*, 1981; Kauffman & Fürsich, 1982; Bottjer, 1986; Diner, 1986; Gautier, 1986; Sageman, 1986; Watkins, 1986; Wright, 1987; Dean *et al.*, 1988). The regional palaeogeography established a precipitation gradient across the seaway. Runoff from the west diluted its surface waters, thereby possibly killing bryozoan larvae entering the seaway from other regions. Evaporation in the east increased salinity, hence density, and this created a sluggish bottom flow back down-slope, and eventually an upwelling enhancing productivity. Phytoplankton and terrigenous sediment both made for murky waters; decay of terrestrial plant and phytoplanktonic debris depleted oxygen in the seaway's bottom waters. This combination of elevated salinity, high turbidity, very soft muddy bottoms, and poor circulation would have been lethal for most bryozoan colonies, except those on the refuges provided by giant shells or free-swimming ammonites.

Recently, an additional explanation is suggested by modelling Cretaceous oceanic circulation (Barron & Peterson, 1989, 1990), which suggests that prevailing surface currents flowed away from North America and towards Europe, a pattern which would prevent bryozoan larvae from being transferred westward out of the high diversity European region. An interesting comparison might be made with

W   **E**

HUMID   WESTERN   DRY
HIGHLANDS   INTERIOR   PLAINS
                               SEAWAY

ON AMMONITES

freshwater   evaporation
run-off

                               brackish surface water   increasing
BRYOZ   *BRYOZ*   salinity
ON   *plant*   mud   *phytoplankton*   ● *BRYOZ*
OYSTERS   *debris*   *rain*   **BRYOZ** *ON SHELL ISLANDS*

                               oxygen-deficient   high turbidity
                          upwelling   *slightly hypersaline*   soupy substrates
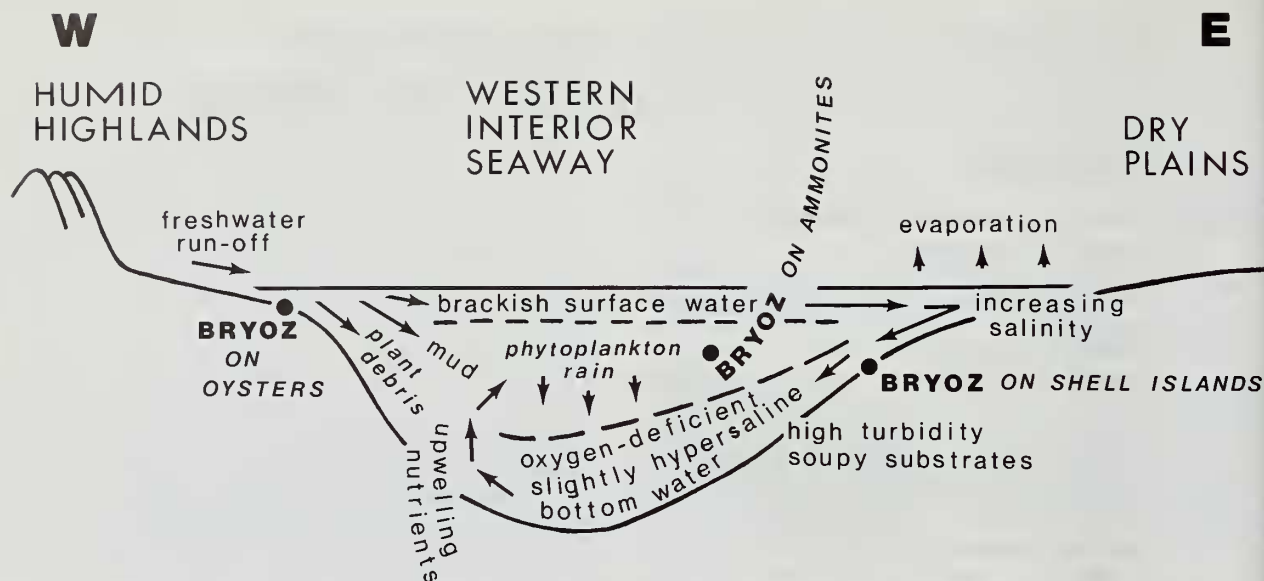   *nutrients*   *bottom water*

Fig. 1   Schematic cross section of the Western Interior Cretaceous Seaway showing regional palaeoenvironmental factors interacting to produce local habitat effects severely limiting bryozoan development, except where indicated by 'BRYOZ'. Western shoreline bryozoan occurrence exemplified by this paper and Cuffey *et al.* (1981); central occurrence by Cuffey (1990) and Gill & Cobban (1966); eastern occurrence by Kauffman (1986).

present-day reef corals in the Indo-Pacific; Jokiel (1989) has suggested that movement of rafted corals and drifted larvae occurs predominantly away from peripheral areas of low coral diversity (cf. Western Interior seaway) and towards centres of high diversity (cf. Europe) which act as areas of species accumulation. However, there is as yet no good evidence from temporal and geographical distributions to suggest that regions like the Western Interior seaway were source areas for the large numbers of bryozoan species present in Cretaceous rocks of Europe.

Another observation which may have some bearing on the low diversity of bryozoan species in the Western Interior is that most (or all) of the cheilostome species described lack ovicells and can therefore be inferred to have possessed long-lived, planktotrophic, cyphonautes larvae (see Taylor, 1987, 1988). This contrasts with the European Upper Cretaceous where the great bulk of species have ovicells and consequently possessed short-lived, non-planktotrophic, coronate larvae. Rates of speciation are predicted to have been higher in non-planktotrophic groups than in planktotrophic groups (Taylor, 1988), and it may also be significant that planktotrophic groups at the present day are subordinate to non-planktotrophic groups in most environments except nearshore and estuarine environments—as noted below (p. 16), the Drumheller bryozoans come from a brackish environment.

GEOLOGICAL SETTING

Location and localities

The bryozoans studied herein come from near Drumheller in central Alberta, western Canada, where the Red Deer River has incised a valley 120 m (400 ft) below the surrounding

plains (Figs 2 & 3). Specific localities are as follows:

1. *Horseshoe Canyon (HS).* Badlands and elongate ravine draining northward into Kneehills Creek (tributary to the Red Deer River), 13·3 km (8·3 miles) west-southwest of the bridge carrying Alberta Highway 9 over the Red Deer River in the centre of Drumheller. Bryozoans (types of *Eokotosokum bicystosum*) on rare oyster shells obtained 3·5 km (2·2 miles) N25°W of parking viewpoint where Alberta Highway 9 runs along the badlands rim (Fig. 3A). Bryozoan locality at Universal Transverse Mercator coordinates 5700900 m N, 368000 m E, in the western branch of this canyon, as marked on the 1990 Drumheller 1:50,000 topographic map (Energy Mines & Resources Canada); land survey coordinates SW corner SE1/4 sec. 33, Tp. 29 [not 28], R.21W4.

2. *Horsethief Canyon (HT).* Badlands forming eastern side of Red Deer River valley, 13·7 km (8·5 miles) northwest of the provincial Highway 9 bridge across the Red Deer River in the centre of Drumheller. Bryozoans on abundant oyster fragments in thin lens at 756 m (2480 ft) elevation, on north side of badlands hill (Fig. 3B) located 200 m (650 ft) S45°W of parking viewpoint where gravel road ends at rim of valley. Bryozoan locality at Universal Transverse Mercator coordinates 5711600 m N, 370500 m E, as marked on the 1989 Munson 1:50,000 topographic map (Energy Mines & Resources Canada); land survey coordinates centre E1/2 NE1/4 sec. 34, Tp. 30, R.21W4.

3. *Drumheller area (DR).* Badlands and tributaries along the Red Deer River valley near Drumheller. Bryozoans on oyster shells found by various amateur and commercial collectors in the area; precise locality details unavailable.

Stratigraphy and palaeoecology

The Drumheller bryozoans are found in the lower oyster bed of the Drumheller marine tongue coming into the Horseshoe

Canyon Formation of the Edmonton Group (Jackson *et al.*, 1981; Harvey *et al.*, 1982; Irish, 1970; Stelck *et al.*, 1972; Allan & Sanderson, 1945). The tongue is of early Maastrichtian age, and thus is near (but not exactly at) the top of the Upper Cretaceous series here (Fig. 4). The regional stratigraphy is characterized by diachronous intertonguing of the major lithofacies. These were deposited along a deltaic shoreline retreating southeastwards, but frequently fluctuating locally in response to variations in sediment supply, coastal-ground compaction or subsidence, regional tectonism, and possibly also eustatic sea-level changes.

The great bulk of the Edmonton Group is made up of the Horseshoe Canyon Formation, 275 m (900 ft) thick around Drumheller, and consisting of complexly interlensing and interbedded grey, tan and brown shales, mudstones, and soft sandstones, with scattered thin lenses of concretionary ironstone and several beds of subbituminous coal. It is overlain by the thin Whitemud Sandstone, Battle Shale, and dinosaur-bearing Scollard Beds. It is underlain by the fully marine, but shallow water, dark-grey Bearpaw Shale, 150 m (500 ft) thick in this vicinity; their contact is an intertonguing transitional zone, and the Drumheller marine tongue is simply a somewhat later and more extensive part of this formational interface on a regional scale (Fig. 4). The Horseshoe Canyon Formation has yielded various continental fossils: dinosaurs, small vertebrates, freshwater molluscs, woody plants, and palynomorphs (Allan & Sanderson, 1945; Irish, 1970; Srivastava, 1970; Harvey *et al.*, 1982; Gross, 1985). These indicate a humid subtropical climate at the time when *Eokotosokum bicystosum* inhabited the adjacent bays. Especially in its lower portion transitional into the Bearpaw Shale, the Horse-
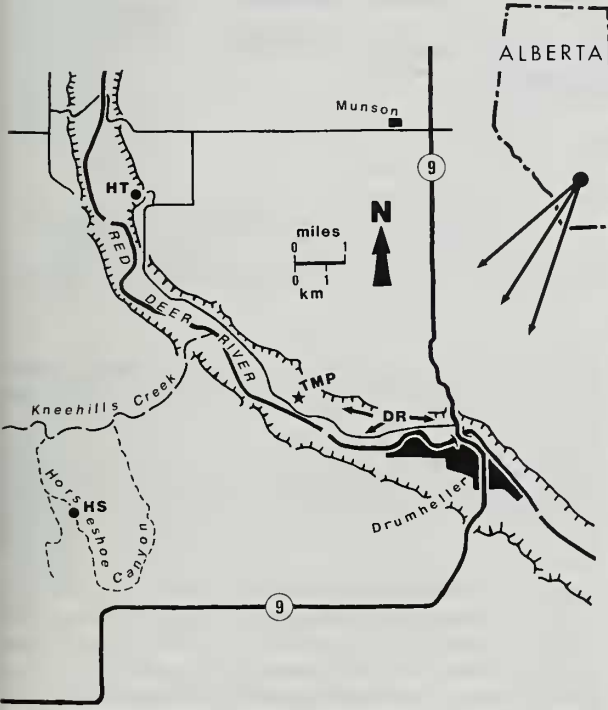

A

B

Fig. 3 Views of Drumheller bryozoan localities. A, locality HS. B, locality HT. Arrows indicate positions of collecting sites within the intricately sculptured badlands, as seen from the parking viewpoints where the footpaths to the sites begin.

Fig. 2 Sketch map of the Drumheller region, central Alberta, Canada, showing bryozoan localities HS, HT and DR (see text), Tyrrell Museum of Palaeontology (TMP), and rim of valley badlands at edge of the flat plains above the Red Deer River.

shoe Canyon Formation represents deposition in a continental to paralic delta complex, with many different subenvironments recognizable (Irish, 1970; Shepheard & Hills, 1970; Harvey *et al.*, 1982; Rahmani & Hills, 1982; Waheed & Miall, 1985).

The badlands and valley wall at locality HT are made up entirely of the Horseshoe Canyon Formation (Jackson *et al.*, 1981; Stelck *et al.*, 1972). Most of the exposures at locality HS
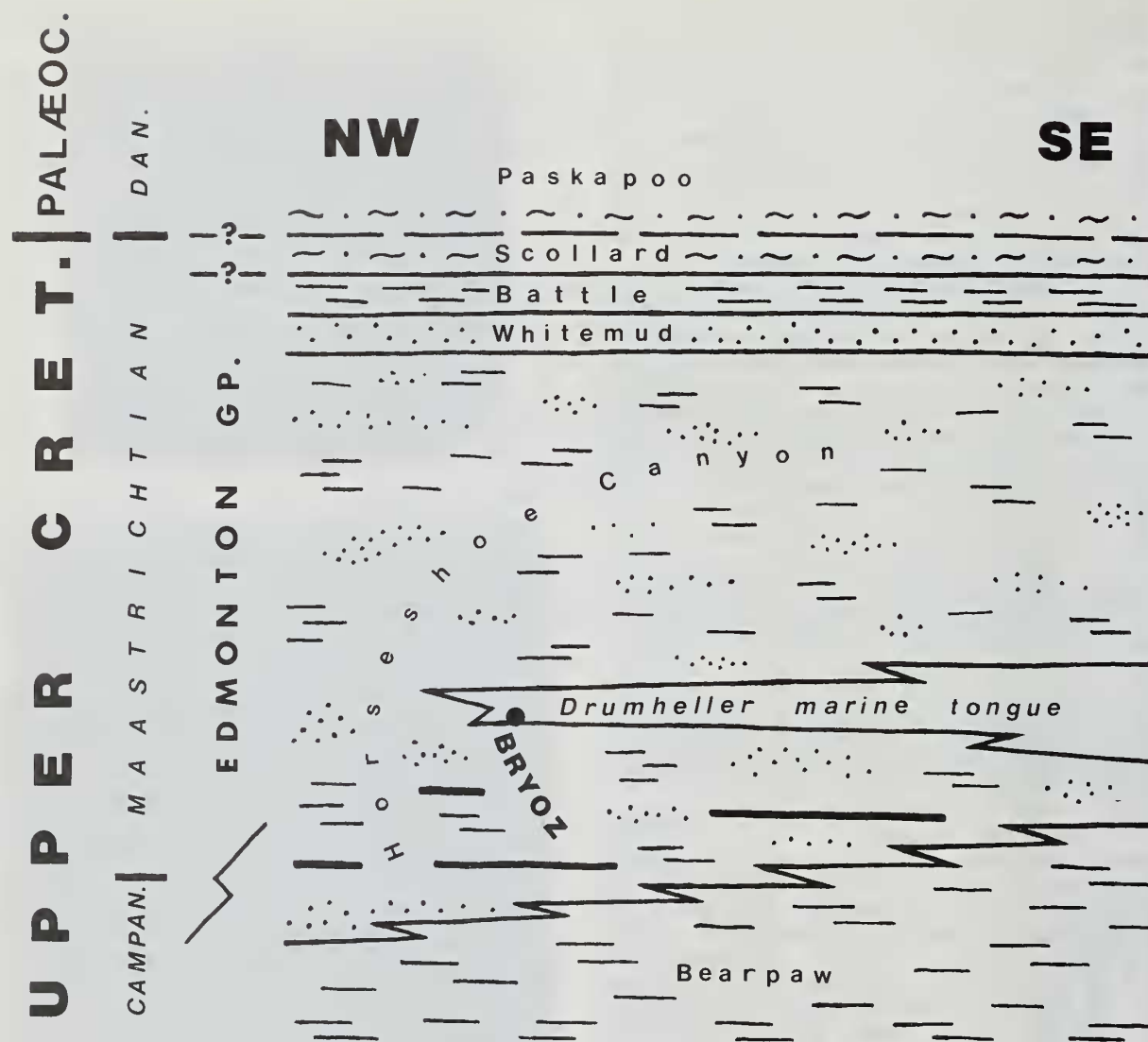
Fig. 4 Diagrammatic summary of stratigraphical relationships of bryozoan-bearing beds near Drumheller; 'BRYOZ' indicates stratigraphical position of localities HS, HT and DR.

are the same formation also, but the Whitemud, Battle and basal Scollard Formations form the highest rim at the lip of the plains upland surface.

At both bryozoan-bearing localities examined (HS – Allan & Sanderson, 1945: 57; Irish, 1970: 134–5; HT – RJC personal observations), the Drumheller marine tongue consists of a thin (0·3–1·0 m = 1–3 ft) lower oyster shell-bed entirely of *Crassostrea glabra coalvillensis* (some encrusted by *Eokotosokum bicystosum*) in a silt matrix, a middle unfossiliferous mudstone (5–6 m = 15–18 ft), and an upper sandstone (0·3–1·0 m = 1–3 ft) with fragmentary *Corbicula occidentalis ventricosa* (but no encrusting bryozoans). Elsewhere, the tongue is structured differently and contains other brackish or marine molluscs, ray-teeth, fish-scales, and even foraminiferans (Allan & Sanderson, 1945; Irish, 1970: 136–7; Stelck *et al.*, 1972: 18–19, 46–8). These deposits represent short-lived, temporary, brackish bays or estuaries indenting the overall deltaic coastline. Modern environmental analogues can be seen along the coats of Louisiana (Shepheard & Hills, 1970: 208) and Georgia (Rahmani & Hills, 1982: 4, 9, 16, 19).

The bryozoan–oyster beds and lenses within the Drumheller tongue were actually brackish estuarine rather than euhaline marine, as indicated by the extremely low diversity of their fauna. All but one of the many Drumheller bryozoan colonies represent the single species *Eokotosokum bicystosum*, and virtually all of the shells occurring with them are the one oyster *Crassostrea glabra coalvillensis*. None of the shells collected in place were bored, unlike some of the North Dakota bryozoan-encrusted oysters with possible ctenostome (*Orbignyopora*) or phoronid (*Talpina*) borings (Cuffey *et al.*, 1981). Such a low-diversity oyster–bryozoan assemblage closely resembles that of Pleistocene and Recent Atlantic coastal estuaries where the abundant oyster *Crassostrea virginica* bears crusts of only three or so membraniporoid species (Mapleton & Cuffey, 1992; Butler & Cuffey, 1991;

Kent, 1988; Osburn, 1944; Winston, 1977).

Finally, note must be taken of a surprising peculiarity endemic to Drumheller stratigraphic literature: namely, calling the oyster shell fragments 'ostracods' (even as recently as Harvey *et al.*, 1982: 3–4, 18).

Preservation and methods

Preservation of bryozoans encountered in the Western Interior Cretaceous varies enormously from site to site. Some localities yield obscure remnants identifiable only to family, like the bryozoans found on baculitid ammonites in Colorado and Wyoming (Cuffey, 1990; Gill & Cobban, 1966). Others furnish moderately well-preserved calcareous skeletal fossils, such as those encrusting oysters in North Dakota and Kansas (Cuffey *et al.*, 1981; Scott, 1970). The Drumheller bryozoans exemplify the latter style of preservation, and so can be studied using techniques like scanning electron microscopy now standard in bryozoology (Taylor, 1990). The capability of scanning uncoated specimens using back-scattered electron imaging (Taylor, 1986*a*) has made detailed study and accurate illustration of the type specimens of *Eokotosokum bicystosum* possible.

SYSTEMATIC PALAEONTOLOGY

Specimen repositories and abbreviations. Materials examined for this paper are housed in the following collections: BMNH, The Natural History Museum, London; PBRC-PSU, Paleobryozoological Research Collection at Pennsylvania State University, University Park, State College, Pennsylvania; ROM, Royal Ontario Museum, Toronto; SMC, Sedgwick Museum, Cambridge; TMP, Tyrrell Museum of Palaeontology, Drumheller; USNM, National Museum of Natural History, Smithsonian Institution, Washington.

Order **CHEILOSTOMIDA** Busk, 1852
Suborder **MALACOSTEGINA** Levinsen, 1902
Superfamily **MEMBRANIPOROIDEA** Busk, 1854
Family **ELECTRIDAE** Stach, 1937

Genus *EOKOTOSOKUM* nov.

TYPE SPECIES. *Conopeum bicystosum* Allan & Sanderson, 1945; Lower Maastrichtian, central Alberta, Canada.

NAME. *Eokotosokum* is a classicized version of the Blackfoot Indian word-combination meaning ancient stone sheets, alluding to the encrusting sheet-like form of the colonies. The Blackfeet were the overall tribe ranging through the type region in aboriginal times.

DIAGNOSIS. Electrid genus with autozooids having a shelf-like, pustulose cryptocyst, an imperforate gymnocyst and a pair of large distolateral spine bases; pore chambers apparently absent; ancestrula budding a distal and a proximal periancestrular zooid; colonies sheet-like, initially uniserial but predominantly multiserial, unilamellar or thinly multilamellar.

REMARKS. This new genus is proposed because *Conopeum bicystosum* is sufficiently distinctive from, and cannot be easily assigned to, any existing genus of cheilostomes.

The lack of ovicells in any of the large suite of specimens available implies that *Eokotosokum bicystosum* possessed non-brooded, planktotrophic larvae. Therefore, the species belongs to a primitive, paraphyletic grouping of anascan cheilostomes termed 'malacostegans' (Taylor, 1987). The occurrence of a proximal periancestrular bud, a feature lost in the great majority of advanced brooding cheilostomes, further supports this interpretation, and lack of a twinned ancestrula allows assignment to the more primitive of the two currently recognized malacostegan families, the Electridae.

Comparison with the type species of existing nominal genera of 'malacostegan' cheilostomes reveals significant differences between these and *Eokotosokum*. The pertinent genera with similar colony and zooid morphologies are *Conopeum*, *Charixa*, *Spinicharixa*, *Wawalia*, *Electra* and *Biflustra* (see Taylor, 1987) and *Villicharixa* Gordon, 1989. *Eokotosokum* shares with the type species of *Conopeum*, the Recent *C. reticulum* (Linnaeus), a reduced gymnocyst, a broad pustulose cryptocyst, and the absence of pore chambers. However, the two genera differ in the presence of prominent spine bases in *Eokotosokum*, closure plates in *Conopeum*, and in details of their early budding pattern: the ancestrula of *Conopeum* buds a proximal and two distolateral zooids whereas that of *Eokotosokum* buds a proximal and one distal zooid. The type species of *Charixa*, *C. vennensis* Lang from the Albian, is poorly known (Taylor, 1986*b*), but it and other species assigned to *Charixa* have better-developed gymnocysts and less well-developed cryptocysts than *Eokotosokum*. Although distolateral spine bases occur sporadically in zooids of *Charixa lindiensis* Taylor, resembling those of *Eokotosokum*, species of *Charixa* possess pore chambers which are absent in *Eokotosokum*. *Spinicharixa*, type species *S. pitti* Taylor from the Lower Cretaceous, has multiple spine bases surrounding the opesia (see p. 22), and closure plates, and the ancestrula buds only a distal zooid. Early budding pattern in *Wawalia*, type species *W. crenulata* Dzik from the Lower Cretaceous, also differs from that observed in *Eokotosokum*, and *Wawalia* is further distinguished by striations on the cryptocyst and its fissured gymnocyst. *Electra*, type species the Recent *E. verticillata* (Ellis & Solander)(= *E. pilosa* (Linnaeus)), shares with *Eokotosokum* a 'compound multiserial' growth-form (Silén, 1987), but again differs in early budding pattern and also lacks a cryptocyst and distolateral spine bases, and has a porous gymnocyst. Finally, *Biflustra*, type species the Recent *B. savartii* (Audouin), differs from *Eokotosokum* in having no gymnocyst and, importantly, in possessing a twinned ancestrula. *Villicharixa*, type species *Membraniporina strigosa* Uttley from the Pleistocene and Recent of New Zealand, has multiple spine bases and a poorly-developed cryptocyst (see p. 22).

These comparisons provide justification for the proposal of the new genus *Eokotosokum*. Although initially monospecific, restudy of the diverse but poorly-known membraniporimorph cheilostomes of Cretaceous to Recent age can be expected to reveal additional congeneric species.

Eokotosokum bicystosum (Allan & Sanderson, 1945)
Figs 5–12
1931 *Conopeum bicystosum* Sanderson: 1254 [nomen nudum].
1945 *Conopeum bicystosum* Allan & Sanderson: 89; pl. 7.

HOLOTYPE. ROM 5337.ct.(a); Drumheller marine tongue,

Horseshoe Canyon Formation, Edmonton Group (lower Maastrichtian); locality HS, near Drumheller, Alberta; J.O.G. Sanderson Collection. Although Allan & Sanderson (1945) mentioned only a holotype specimen under this registration number, the ROM collections contain two specimens, encrusting separate oyster shells, labelled as cotypes (i.e. syntypes). One of these specimens (Fig. 7) corresponds closely with their illustration (1945: pl. 7) which is, however, reproduced upside down; this specimen is taken to be the intended holotype.

PARATYPE. The second specimen in the ROM Collection – 5337.ct.(b) – includes a less well-preserved colony of *E. bicystosum*, interpreted as a paratype, together with the colony of *Villicharixa lintonensis* described below.

OTHER MATERIAL. BMNH D57396–401, D59482–3, locality DR; TMP 91.136.1 and 91.136.2, locality DR; TMP 91.136.3, locality HT; PBRC-PSU ALBDRU-DR and ALBDRU-HT suites, localities DR and HT respectively. All from the Drumheller marine tongue, Horseshoe Canyon Formation, Edmonton Group (lower Maastrichtian), near Drumheller, Alberta, Canada.

DESCRIPTION. Colonies are encrusting, sheet-like (Figs 5A, 8A), initially uniserial (Figs 9A, 10) but predominantly multiserial, unilamellar or thinly multilamellar (Fig. 6). All available specimens are incomplete colonies characteristically preserved as irregular patches of 10 or more zooids encrusting oyster shells, abraded at patch edges, and representing portions of larger, fragmented colonies. Recognizable growing edges have not been observed. The rarely visible early zooids are arranged in two uniserial branches originating from the distal and proximal ends of the ancestrula (Figs 9, 10). Distolateral budding from post-ancestrular zooids causes multiplication of branch number to give a multiserial colony of the compound type (*sensu* Silén, 1987); intact colonies may have been roughly circular in outline and centred on the ancestrula. In multiserial unilamellar colonies, zooids are arranged in several series paralleling colony growth direction. Zooids of adjacent rows tend to alternate, thus yielding an approximately quincuncial pattern. Multilamellar colonies (Fig. 6) are common and apparently develop by intracolonial overgrowth but do not attain massive thicknesses. Zooids in overgrowths are typically more irregular in shape (some even having re-entrant angles), more disorderly in arrangement and more loosely-packed than are zooids in the basal layers of colonies.

Autozooids have a longitudinally elongate, ovoidal to rectangular outline shape, about 1·5 times as long as wide, and are moderately small (Table 1). Most of the frontal area of the zooid is occupied by the opesia which is also longitudinally ovoidal in shape but is slightly square-ended in most zooids (Figs 5B, 8B). The cryptocyst forms a well-defined shelf around the opesia and is generally at its broadest proximally and narrowest distally. Proximal and lateral parts of the cryptocyst slope gently inwards, whereas the distal part is more steeply sloping. Prominent, evenly-sized pustules are arranged in 6 or more alternating rows on the cryptocyst (Fig. 8B). The gymnocyst forms a small area of smooth calcification outside the cryptocyst. It is usually most extensive proximally and is reduced laterally and distally to a narrow zone dipping steeply into the furrows that separate the zooids. A distolateral pair of spine bases occurs on the cryptocyst–gymnocyst boundary, indenting the cryptocyst

and apparently causing the square-ended shape of the opesia (Fig. 11). They are crater-like in form, large (about 0·03 mm maximum diameter), and elongated parallel to the cryptocyst–gymnocyst boundary and hence sub-transversely or obliquely to the long axis of the zooid. The basal walls of at least some zooids are completely calcified. Pore chambers have not been observed in spite of the presence of numerous abraded zooids in which they should be visible if developed. Closure plates are absent. Ovicells do not occur. Intramural buds ('regenerations') are moderately uncommon and are recognizable by the occurrence of a secondary ring-like cryptocyst inside that of the host zooid (Fig. 5B). Some intramural buds have a greater height than the host zooid. These eruptive buds are possible origins of intracolony overgrowths. Whereas eruptive intramural buds possess spine bases and appear to be autozooids, the few observed non-eruptive intramural buds lack spine bases and may be kenozooids. The polarity of eruptive intramural buds, determined by the position of the spine bases, can be oblique to that of the host zooid.

The ancestrula is small (Table 1), longitudinally ovoidal in outline, and has a subcircular opesia which occupies over half of the frontal area (Fig. 9B). Like the post-ancestrular zooids, it has a pustulose, shelf-like cryptocyst, an inextensive gymnocyst best developed proximally, and a pair of distolateral spine bases. However, an additional pair of spine bases appears to occur proximolaterally in one partly sediment-obscured ancestrula and in its daughter zooids. The ancestrula gives rise to two periancestrular daughter zooids, one distally and one proximally. These early zooids initiate a primary zone of astogenetic change, encompassing at least six generations, through which zooid size increases progressively.

Kenozooids and putative kenozooids of varying types can be distinguished by their lack of spine bases, and generally smaller size, irregularity and reduced calcification compared to autozooids. Some are 'vicarious' (Fig. 12B), intercalated in the normal budding sequence of the autozooids, but in areas where spatial restrictions seem to have prohibited autozooid formation; others are distinctly 'adventitious' (Fig. 12A) and occupy interopesial areas on the colony surface, while some appear to be intermediate in that they have small bases in contact with the substratum but expand frontally across interopesial areas. A single large vicarious kenozooid (Fig. 12B) has been observed in which the cryptocyst is substantially broadened distally. Some of the adventitious

Table 1 Zooidal dimensions (mm) in *Eokotosokum bicystosum* (Allan & Sanderson). All measurements of post-ancestrular zooids are from the holotype colony. Abbreviations: x̄ = mean; r = observed range; SD = standard deviation; CV = coefficient of variation; N = number of zooids measured.

|	x̄	r	SD	CV	N
zooidal length	0·407	0·33–0·53	0·046	11·4	15
zooidal width	0·277	0·23–0·38	0·034	12·3	15
opesial length	0·290	0·26–0·32	0·017	5·8	15
opesial width	0·174	0·12–0·21	0·021	12·1	15
ancestrular length	0·16	0·16	–	–	3
ancestrular width	0·13	0·12–0·14	–	–	3
ancestrular opesial length	0·09	0·09	–	–	2
ancestrular opesial width	0·09	0·09	–	–	2
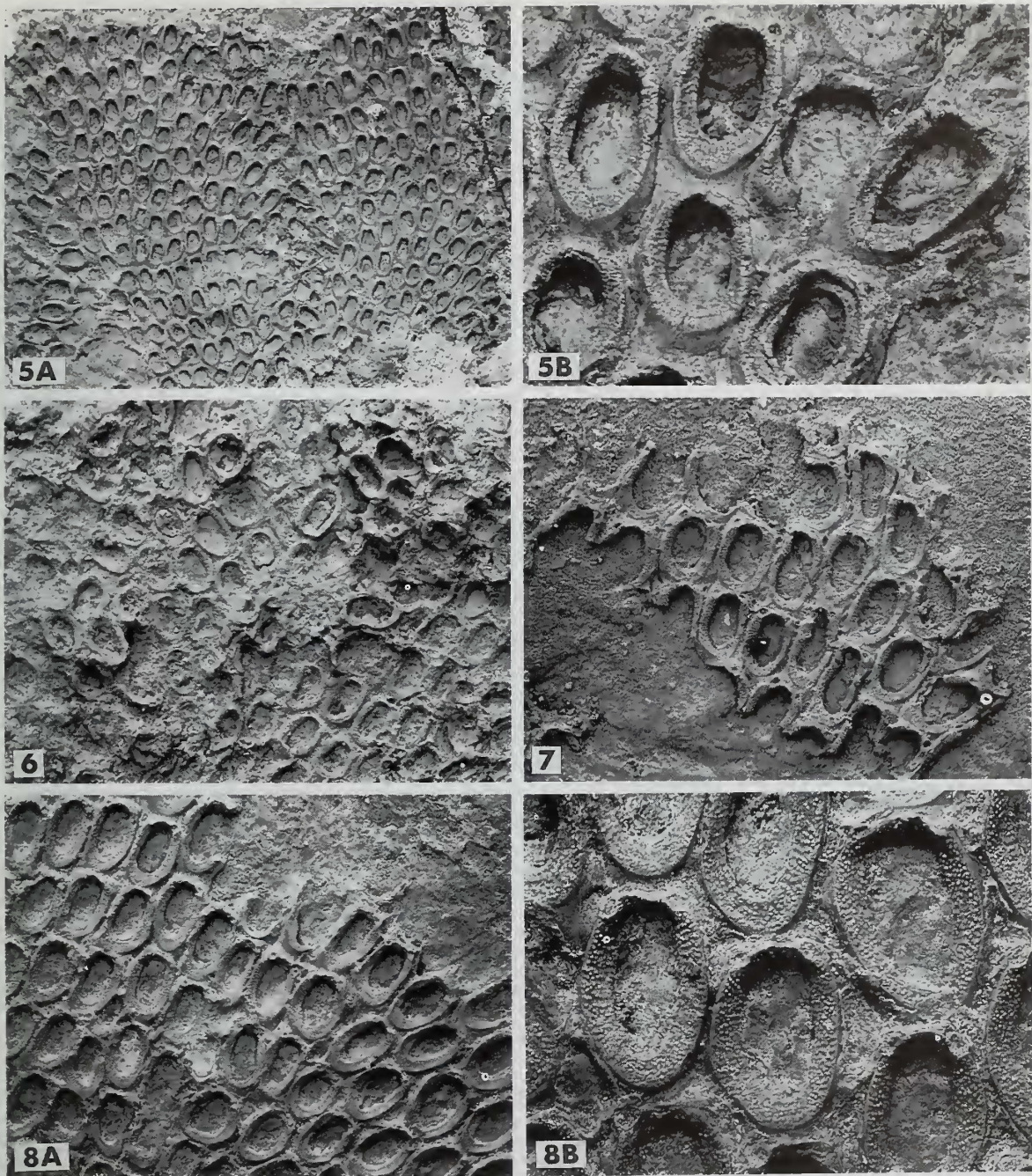
Figs 5–8 *Eokotosokum bicystosum* (Allan & Sanderson), L. Maastrichtian, Edmonton Group, Horseshoe Canyon Formation, Drumheller marine tongue; Drumheller area, Alberta. Scanning electron micrographs of uncoated specimens imaged using back-scattered electrons. Fig. 5, TMP 91.136.1 (see also Fig. 12); 5A, part of a large colony, × 12; 5B, autozooids, one (centre bottom) with a 'regeneration', × 85. Fig. 6, TMP 91.136.2 (see also Fig. 9), colony with overgrowths, × 25. Fig. 7, ROM 5337.ct.(a), part of the holotype colony, × 35. Fig. 8, BMNH D57396 (see also Fig. 11); 5A, autozooids and kenozooids near broken edge of colony, × 27; 5B, autozooids showing pustulose cryptocysts, × 80.

and intermediate kenozooids lack both gymnocysts and pustulose cryptocysts, and possess only basal walls and reduced vertical walls; abrasion may have accentuated the vestigial morphology of these kenozooids. A second possible source of multilamellar colony growth could be budding from adventitious and intermediate type kenozooids.

Avicularia are absent.

REMARKS. The original description of *E. bicystosum* by Allan & Sanderson (1945) is reasonably accurate but fails to
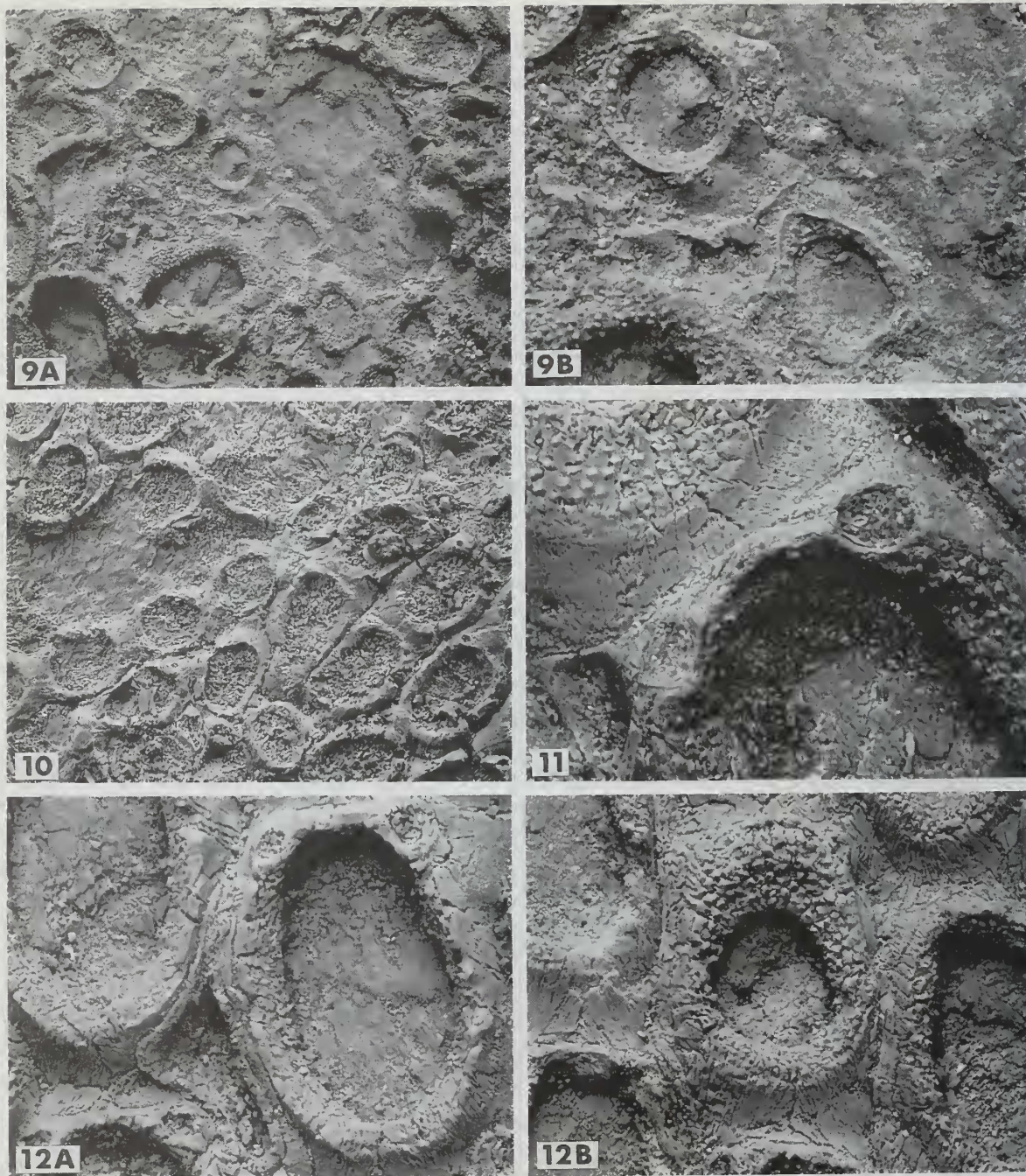
Figs 9–12 *Eokotosokum bicystosum* (Allan & Sanderson), L. Maastrichtian, Edmonton Group, Horseshoe Canyon Formation, Drumheller marine tongue; Drumheller area, Alberta. Scanning electron micrographs of uncoated specimens imaged using back-scattered electrons. Fig. 9, TMP 91.136.2 (see also Fig. 6); 9A, early zooids arranged in a uniserial line running top left to bottom right of the micrograph, × 70; 9B, ancestrula (top left) with proximal bud (bottom right), × 170. Fig. 10, TMP 91.136.3, early zooids of another colony, × 56. Fig. 11, BMNH D57396 (see also Fig. 8), large distolateral spine bases of an autozooid, × 310. Fig. 12, TMP 91.136.1 (see also Fig. 5), kenozooids; 12A, small kenozooid with reduced calcification infilling area between autozooids, × 180; 12B, large, vicarious kenozooid, × 173.

identify the occurrence of the large distolateral spine bases which are very characteristic of the species and presumably signify the presence during life of substantial upright or perhaps overarching spines in the orificial region. Although it

is possible that Allan & Sanderson described the spine bases as interopesial spaces, this description could equally apply to the adventitious kenozooids. Many of the morphological features of this and similar cheilostomes cannot be ade-

quately resolved using an optical microscope and full description demands the use of scanning electron microscopy.

Only one other formally described cheilostome species is known to occur in the uppermost Cretaceous of the Western Interior province. This is *Villicharixa lintonensis* (Cuffey, Feldmann & Pohlable, 1981), distinguished from *E. bicystosum* by the presence of a gymnocystal tubercle on the proximal edge of the opesia, multiple small spine bases encircling the opesia, a negligible cryptocyst, and a different early budding pattern (see p. 22). Elsewhere, Upper Cretaceous membraniporimorph bryozoans have been described from the Ripley Formation of Tennessee (Canu & Bassler, 1926), and from many localities in Europe (e.g., see Voigt, 1979, 1981, 1983). Few of these species possess distolateral spine bases of the type characterizing *E. bicystosum*. *Membranipora gegania* Brydone, from the lower Maastrichtian of Norfolk, England, does have a distolateral pair of spine bases, but study of the holotype (SMC B36555) has revealed several differences from *E. bicystosum*: the autozooids in *M. gegania* are larger and broader, small ovicells are present, and large pore chambers occur. *Membranipora frontalis*

Levinsen, described from the lower Maastrichtian of Denmark, seems also to have broader autozooids than *E. bicystosum* and apparently possesses pore chambers; it may be a senior synonym of *M. gegania*..

DISTRIBUTION. Drumheller marine tongue, Horseshoe Canyon Formation, Edmonton Group (lower Maastrichtian); localities HS, HT and DR, near Drumheller, Alberta, Canada. Also recorded by Sanderson (1931: 1254) and Allan & Sanderson (1945: 79) from the Fox Hills Sandstone (lower to middle Maastrichtian) of southern Alberta; however, this record requires confirmation as the specimens have not been figured and may alternatively be *Villicharixa lintonensis*.

Genus *VILLICHARIXA* Gordon, 1989

TYPE SPECIES. *Membraniporina strigosa* Uttley, 1951, by original designation (Gordon, 1989); Pleistocene and Recent of New Zealand.
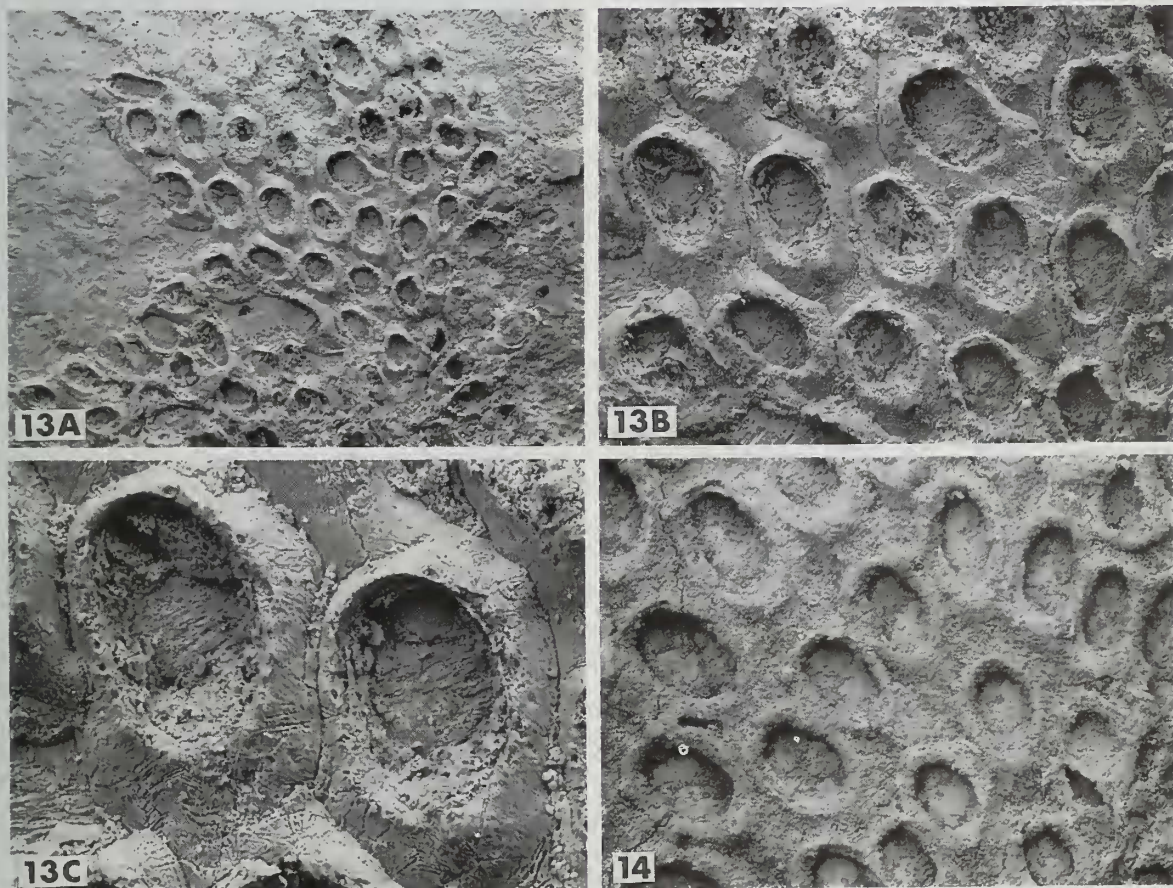
Figs 13–14 *Villicharixa lintonensis* (Cuffey, Feldmann & Pohlable). Fig. 13, ROM 5337.ct.(b), L. Maastrichtian, Edmonton Group, Horseshoe Canyon Formation, Drumheller marine tongue; Drumheller area, Alberta. Scanning electron micrographs of uncoated specimen imaged using back-scattered electrons; 13A, general view of colony encrusting the same substrate as the paratype of *Eokotosokum bicystosum*, × 20; 13B, irregularly-arranged autozooids, × 60; 13C, two autozooids showing numerous small spine bases around the opesiae, × 127. Fig. 14, USNM 263780, Maastrichtian, Fox Hills Sandstone, Timber Lake Member; locality 3 of Cuffey *et al.* (1981), Emmons County, North Dakota. Scanning electron micrographs of coated holotype specimen imaged using back-scattered electrons; compare with Fig. 13B, × 60.

REMARKS. Gordon (1989) erected *Villicharixa* to accommodate some austral Quaternary electrid species resembling *Spinicharixa* Taylor, 1986b, in having numerous spines surrounding the opesia but lacking pore chambers. Unfortunately, the early astogeny of the type species of *Villicharixa* is not known. Gordon additionally referred *Electra pilosissima* Moyano to *Villicharixa*, and a third species, *Electra ongleyi* Brown (Fig. 15), also appears to belong to this genus. The assignment herein to *Villicharixa* of *Wilbertopora? lintonensis* Cuffey, Feldmann & Pohlable, 1981 from the Maastrichtian of North America not only extends considerably the geological and geographical range of the genus, but also provides the first details of early astogeny in the genus.

Villicharixa lintonensis (Cuffey, Feldmann & Pohlable, 1981)

Figs 13–14

1981   *Wilbertopora? lintonensis* Cuffey, Feldmann & Pohlable: 404–408; text-fig. 3A–C; pl. 1, figs 1–2.

MATERIAL. ROM 5337.ct.(b); Drumheller marine tongue, Horseshoe Canyon Formation, Edmonton Group (lower Maastrichtian), locality HS, near Drumheller, Alberta; J.O.G. Sanderson Collection. A colony partially overgrown by the paratype of *Eokotosokum bicystosum*.

DESCRIPTION. Colonies are encrusting, sheet-like (Fig. 13A), multiserial and unilamellar, the zooids rather irregularly arranged (Fig. 13B). Early growth stages are not observable in the Drumheller specimen (but see Remarks).

Autozooids have an elongate ovoidal or subrhomboidal outline shape, about 1·7 times as long as wide (Table 2). One abnormally broad autozooid may be a 'doppelzooid' (Jebram & Voigt, 1977) formed by bud fusion. The opesia is ovoidal, longer than wide, and occupies about half of the frontal length of the zooid. Numerous small spine bases surround the opesia (Fig. 13C). Incomplete preservation prohibits their exact number from being counted, but there may be up to 16, the most distal pair being especially prominent. Cryptocysts are absent. The gymnocyst is well developed, particularly proximally. Laterally and distally of the opesia, it forms a steeply sloping border descending into the furrow between zooids. A broad gymnocystal tubercle may be present on the proximal edge of the opesia.

Ovicells, kenozooids and avicularia have not been observed.

Table 2   Zooidal dimensions (mm) in *Villicharixa lintonensis* (Cuffey, Feldmann & Pohlable), ROM 5337.ct.(b). Figures in parenthesis are measurements taken from the holotype specimen, USNM 263780 (Fox Hills Sandstone, North Dakota). Abbreviations as in Table 1.

	x̄	r	SD	CV	N
zooidal length	0·494	0·44–0·56	0·038	7·6	10
	(0·533)	(0·50–0·57)	(0·028)	(5·2)	(10)
zooidal width	0·291	0·24–0·35	0·035	12·2	10
	(0·287)	(0·24–0·35)	(0·038)	(13·1)	(10)
opesial length	0·254	0·21–0·30	0·025	9·8	10
	(0·272)	(0·23–0·32)	(0·025)	(9·2)	(10)
opesial width	0·177	0·14–0·20	0·018	10·4	10
	(0·183)	(0·17–0·21)	(0·017)	(9·3)	(10)

REMARKS. This species was originally described from the Maastrichtian Fox Hills Sandstone of North Dakota as *Wilbertopora? lintonensis* by Cuffey *et al.* (1981). The type material of *V. lintonensis* (holotype = USNM 263780; paratypes = USNM 263781–3) has been re-examined using the SEM (Fig. 14), and no significant differences can be detected between it and the specimen from Drumheller. However, the following additions and amendments must be made to the original description of *V. lintonensis*:

1. The small spine bases clearly seen in the Drumheller specimen were not noted in the original description of *V. lintonensis*. They cannot be seen in the Fox Hills Sandstone specimens apparently because of the conditions of their preservation; the holotype specimen is covered by a ferruginous crust which would undoubtedly obscure the spine bases, and the paratypes show only the undersides of colonies.

2. Re-study of paratype specimen USNM 263781, which bears several colonies encrusting the inside of a mollusc, has revealed the ancestrula and early growth stages of *V. lintonensis*. The ancestrula is about 0·14 mm long by 0·09 mm wide, and buds four apparently periancestrular daughter zooids which rapidly establish the multiserial colony-form. The four periancestrular zooids are located one distally, one proximally and two distolaterally.

3. Zooidal dimensions have been re-measured in the holotype (Table 2) and, with the exception of zooidal width, were found to be appreciably larger than the figures quoted by Cuffey *et al.* (1981). In particular, zooidal length averages 0·53 mm rather than 0·37 mm as previously given.

The generic assignment of this species requires explanation. The absence of ovicells and avicularia, and presence of a proximal periancestrular bud, suggest that the species is a 'malacostegan' and is not therefore assignable to the ovicellate 'pseudomalacostegan' genus *Wilbertopora* (type species *W. mutabilis* Cheetham). Among 'malacostegans', the species invites comparison with *Electra* Lamouroux, *Spinicharixa* Taylor, and *Villicharixa* Gordon. The type species of *Electra* (*E. verticillata* = *E. pilosa*) has a periancestrular budding pattern identical to that found in the Maastrichtian species, may also develop spines around the opesia, and similarly lacks a pustulose cryptocyst. However, the gymnocyst in *E. pilosa* is porous, and well-developed pore chambers occur in the early zooids at least. *Spinicharixa* (type species *S. pitti* Taylor) possesses similar multiple spine bases, but the ancestrula buds only a distal periancestrular zooid and pore chambers are present. Although early astogeny is unknown in the type and other species of *Villicharixa*, assignment of the Maastrichtian species to this genus is preferred. *V. lintonensis* closely resembles *V. ongleyi* (Brown) from the ?Pleistocene of New Zealand. The holotype of *V. ongleyi* is re-illustrated here for comparative purposes (Fig. 15). *V. lintonensis* differs from *V. ongleyi* mainly in the presence of a gymnocystal tubercle on the proximal edge of the opesia, and in the poorly-developed cryptocyst, a feature shared with *V. strigosa* (Uttley).

During life the intact spines of *V. lintonensis* would probably have formed a loose, hairy covering to the frontal membrane of the zooids, as in the specimen of *V. strigosa* depicted by Gordon (1989: fig. 2A).

DISTRIBUTION. Drumheller marine tongue, Horseshoe Canyon Formation, Edmonton Group (lower Maastrichtian); locality HS, near Drumheller, Alberta, Canada. Timber Lake and Colgate Sandstone Members, Fox Hills Sandstone
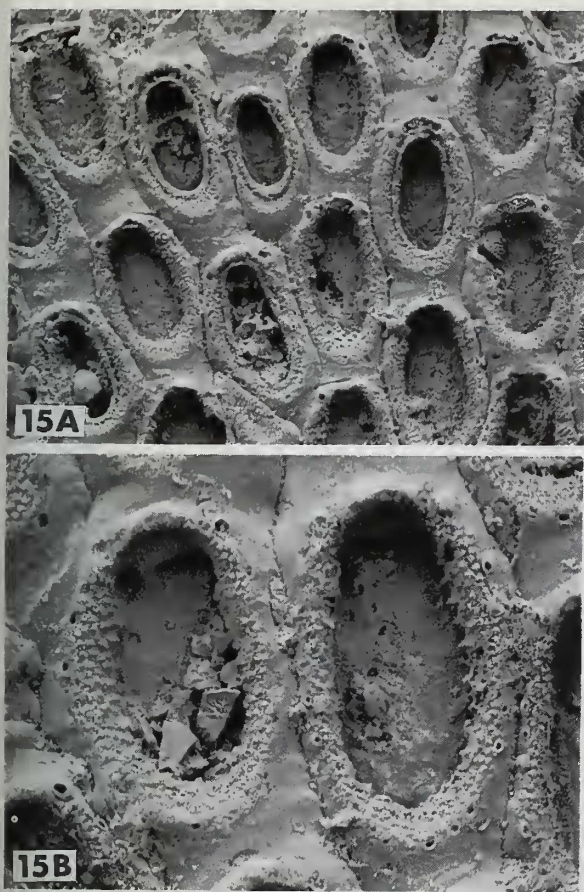
Fig. 15 *Villicharixa ongleyi* (Brown), BMNH D36532, holotype, [probably L. Pleistocene, Petane Limestone], Petane, New Zealand; compare with *V. lintonensis* (Figs 13–14). Scanning electron micrographs of uncoated specimen. 15A, autozooids, some with 'regenerations', × 54; 15B, two autozooids showing numerous small spine bases around the opesiae, × 120.

(middle Maastrichtian); localities near Linton, North Dakota, U.S.A. (Cuffey *et al.*, 1981: 401–2). It is also possible that the bryozoan listed from the Fox Hills Sandstone (lower to middle Maastrichtian) in southern Alberta (Sanderson 1931: 1254; Allan & Sanderson 1945: 79) may represent *Villicharixa lintonensis* rather than *Eokotosokum bicystosum*, as noted above (p. 21).

REFERENCES

Allan, J.A. & Sanderson, J.O.G. 1945. Geology of Red Deer and Rosebud Sheets, Alberta. *Report, Research Council of Alberta*, Edmonton, **13**: 1–115.

Arthur, M.A. & Schlanger, S.O. 1979. Cretaceous 'oceanic anoxic events' as causal factors in the development of reef-reservoired giant oil fields. *Bulletin of the American Association of Petroleum Geologists*, Chicago, **63**: 870–885.

——, Scholle, P.A., Pollastro, R.M., Barker, C.E. & Claypool, G.E. 1981. Geochemical and sedimentologic indicators of depositional environments and diagenetic trends in the Niobrara Formation (Upper Cretaceous), Colorado and Kansas. *Abstracts with Programs, Geological Society of America*, Boulder, Col., **13** (7): 398–399.

Barron, E.J. & Peterson, W.H. 1989. Model simulation of the Cretaceous ocean circulation. *Science*, New York, **244**: 684–686.

—— —— 1990. Mid-Cretaceous ocean circulation: Results from model sensitivity studies. *Paleoceanography*, Washington, **5**: 319–337.

Bottjer, D.J. 1986. Campanian–Maastrichtian chalks of southwestern Arkansas: Petrology, paleoenvironments and comparison with other North American and European chalks. *Cretaceous Research*, London, **7**: 161–196.

——, Roberts, C. & Hattin, D.E. 1978. Stratigraphic and ecologic significance of *Pycnodonte kansasense*, a new Lower Turonian oyster from the Greenhorn Limestone of Kansas. *Journal of Paleontology*, Tulsa, Okla., **52**: 1208–1218.

Busk, G. 1852. An account of the Polyzoa, and sertularian zoophytes, collected in the voyage of the Rattlesnake on the coast of Australia and the Louisiade Archipelago, &c. *In* MacGillivray, J., *Narrative of the voyage of H.M.S. Rattlesnake, commanded by the late Captain Owen Stanley . . . 1846–1850*. **1**: 342–402. London.

—— 1854. *Catalogue of marine Polyzoa in the Collection of the British Museum, II. Cheilostomata (part)*: 55–120. London.

Butler, G.M. & Cuffey, R.J. 1991. Bryozoans as estuarine indicators – Paleoecological implications from the modern fauna of Delaware Bay. *Abstracts with Programs, Geological Society of America*, Boulder, Col., **23** (1): 14.

Canu, F. & Bassler, R.S. 1926. Phylum Molluscoidea. Class Bryozoa. *In* Wade, B., The fauna of the Ripley Formation of Coon Creek, Tennessee. *Professional Paper. United States Geological Survey*, Washington, **193**: 32–37, pls 4–7.

Cuffey, R.J. 1990. Cretaceous bryozoans on Baculite Mesa, Colorado. *Abstracts with Programs, Geological Society of America*, Boulder, Col., **22** (6): 7.

——, Feldmann, R.M. & Pohlable, K.E. 1981. New Bryozoa from the Fox Hills Sandstone (Upper Cretaceous, Maestrichtian) of North Dakota. *Journal of Paleontology*, Tulsa, Okla., **55**: 401–409.

Dean, W.E., Arthur, M.A., Pratt, L.M. & Scholle, P. 1988. Geochemical cycles and events during the Late Cretaceous in the Western Interior seaway of North America – Records of paleoceanographic change. *Abstracts with Programs, Geological Society of America*, Boulder, Col., **20** (7): A197.

Diner, R. 1986. Foraminifera/water-mass relationships across the Cenomanian–Turonian stage boundary. *4th North American Paleontological Convention. Abstracts with Programs*, Boulder, Col.: A12.

Frey, R.W. 1972. Paleoecology and depositional environment of Fort Hays Limestone Member, Niobrara Chalk (Upper Cretaceous), west-central Kansas. *Paleontological Contributions. University of Kansas*, Lawrence, Article **58**: 1–72.

Gautier, D.L. 1986. Cretaceous shales from the western interior of North America: Sulfur/carbon ratios and sulfur-isotope composition. *Geology*, Boulder, Col., **14**: 225–228.

Gill, J.R. & Cobban, W.A. 1966. The Red Bird Section of the Upper Cretaceous Pierre Shale in Wyoming. *Professional Paper. United States Geological Survey*, Washington, **393–A**: 1–73.

Gordon, D.P. 1989. New and little-known genera of cheilostome Bryozoa from the New Zealand region. *Journal of Natural History*, London, **23**: 1319–1339.

Gross, R. 1985. *Dinosaur country: Unearthing the badlands' prehistoric past*. 128 pp. Saskatoon.

Harvey, S., Rivard, G. & Wigham, E. 1982. Ladies' field trip, Drumheller. *Canadian Society of Petroleum Geologists. Field Trip Guidebook*, Calgary, [unnumbered], 27 pp.

Hattin, D.E. 1975. Stratigraphy and depositional environment of Greenhorn Limestone (Upper Cretaceous) of Kansas. *Bulletin. Kansas Geological Survey*, Lawrence, **209**: 1–128.

—— 1982. Stratigraphy and depositional environment of Smoky Hill Chalk Member, Niobrara Chalk (Upper Cretaceous), of the type area, western Kansas. *Bulletin, Kansas Geological Survey*, Lawrence, **225**: 1–108.

Irish, E.J.W. 1970. The Edmonton Group of south-central Alberta. *Bulletin of Canadian Petroleum Geology*, Calgary, **18**: 125–155.

Jackson, P.C. & the Map Committee 1981. *Geological Highway Map of Alberta*. 2nd Edition. Canadian Society of Petroleum Geologists Geological Highway Map Series, Calgary.

Jebram, D. & Voigt, E. 1977. Monsterzooide und Doppelpolypide bei fossilen und rezenten Cheilostomata Anasca (Bryozoa). *Abhandlungen und Verhandlungen des Naturwissenschaftlichen Vereins in Hamburg*, (N.F.) **20**: 151–173.

Jokiel, P.L. 1989. Rafting of reef corals and other organisms at Kwajalein

Atoll. *Marine Biology*, Berlin, **101**: 483–493.

Kauffman, E.G. 1975. Dispersal and biogeographic potential of Cretaceous benthonic Bivalvia in the Western Interior. *Special Papers. Geological Association of Canada*, Toronto, **13**: 163–194.

—— 1986. Structure and microsuccession of hard substrata communities on Mesozoic shell islands. *4th North American Paleontological Convention. Abstracts with Programs*, Boulder, Col.: A23.

—— & Fürsich, F. 1982. Benthic paleocommunity gradients, oxygen levels and source rocks in a Cretaceous epicontinental seaway. *Abstracts with Programs, Geological Society of America*, Boulder, Col., **14** (7): 525–526.

Kent, B.W. 1988. *Making dead oysters talk: Techniques for analyzing oysters from archaeological sites.* 107 pp. St Marys City, Md.

Levinsen, G.M.R. 1902. Studies on Bryozoa. *Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening i Kjøbenhavn*, **54**: 1–31.

Mapleton, L.T. & Cuffey, R.J. 1992. Pleistocene estuarine bryozoans and mollusks at the CEBAF site in southeastern Virginia. *Abstracts with Programs, Geological Society of America*, Boulder, Col., **24** (3): A61.

Osburn, R.C. 1944. A survey of the Bryozoa of Chesapeake Bay. *Publications of the Chesapeake Biological Laboratory*, Solomons Is., Md., **63**: 1–55.

Rahmani, R.A. & Hills, L. 1982. Facies relationships and paleoenvironments of a Late Cretaceous tide-dominated delta, Drumheller, Alberta. *Canadian Society of Petroleum Geologists. Field Trip Guidebook*, Calgary, **6**: 1–43.

Sageman, B.B. 1986. Oxygen-deficient biofacies of the Western Interior Seaway: Evidence from the Hartland Shale Member of the Greenhorn Formation. *4th North American Paleontological Convention. Abstracts with Programs*, Boulder, Col.: A40.

Sanderson, J.O.G. 1931. Fox Hills Formation in Southern Alberta. *Bulletin of the American Association of Petroleum Geologists*, Tulsa, Okla., **15** (10): 1251–1263.

Scott, R.W. 1970. Paleoecology and paleontology of the Lower Cretaceous Kiowa Formation, Kansas. *Paleontological Contributions. University of Kansas*, Lawrence, Article **52**: 1–94.

Shepheard, W.W. & Hills, L.V. 1970. Depositional environments Bearpaw–Horseshoe Canyon (Upper Cretaceous) transition zone, Drumheller 'badlands', Alberta. *Bulletin of Canadian Petroleum Geology*, Calgary, **18**: 166–215.

Silén, L. 1987. Colony growth pattern in *Electra pilosa* (Linnaeus) and comparable encrusting cheilostome bryozoans. *Acta Zoologica*, Stockholm, **68**: 17–34.

Srivastava, S.K. 1970. Pollen biostratigraphy and paleoecology of the Edmonton Formation (Maestrichtian), Alberta, Canada. *Palaeogeography, Palaeoclimatology, Palaeoecology*, Amsterdam, **7**: 221–276.

Stach, L.W. 1937. Lady Julia Percy Island. Reports of the McCoy Society for Field Investigation and Research. 13. Bryozoa. *Proceedings of the Royal Society of Victoria*, Melbourne, (n.s.) **49** (2): 374–384, pl. 22.

Stelck, C.R., Wall, J.H., Williams, G.D. & Mellon, G.B. 1972. The Cretaceous and Jurassic of the Foothills of the Rocky Mountains of Alberta. *24th International Geological Congress Field Excursion Guidebook*, **A20**: 1–51.

Taylor, P.D. 1986a. Scanning electron microscopy of uncoated fossils. *Palaeontology*, London, **29**: 685–690.

—— 1986b. *Charixa* Lang and *Spinicharixa* gen. nov., cheilostome bryozoans from the Lower Cretaceous. *Bulletin of the British Museum (Natural History)*, London, (Geol.) **40**: 197–222.

—— 1987. Skeletal morphology of malacostegan grade cheilostome Bryozoa. *In* Ross, J.R.P. (ed.), *Bryozoa: present and past*: 269–276. Bellingham.

—— 1988. Major radiation of cheilostome bryozoans: triggered by the evolution of a new larval type? *Historical Biology*, London, **1**: 45–64.

—— 1990. The impact of the SEM in studies of living and fossil bryozoans. *In*: Claugher, D. (ed.), *Scanning electron microscopy in taxonomy and functional morphology*: 259–280. London, Systematics Association Special Volume No. **41**.

Uttley, G.H. 1951. The Recent and Tertiary Polyzoa (Bryozoa) in the collection of the Canterbury Museum, Christchurch. Part 2. *Records of the Canterbury Museum*, Christchurch, **6**: 15–39.

Voigt, E. 1979. Vorkommen, Geschichte und Stand der Erforschung der Bryozoen des Kreidesystems in Deutschland und benachbarten Gebieten. *In*: Wiedmann, J. (ed.), *Aspekte der Kreide Europas*. IUGS Series A, **6**: 171–210. Stuttgart.

—— 1981. Répartition et Utilisation Stratigraphique des Bryozoaires du Crétacé Moyen (Aptien–Coniacien). *Cretaceous Research*, London, **2**: 439–462.

—— 1983. Zur Biogeographie der europäischen Oberkreide-Bryozoenfauna. *Zitteliana*, Munich, **10**: 317–347.

Waheed, A. & Miall, A.D. 1985. Depositional framework of Upper Cretaceous fluvio-deltaic coals, south-central Alberta. *Abstracts with Programs, Geological Society of America*, Boulder, Col., **17** (7): 741.

Watkins, D.K. 1986. Nannoplankton productivity fluctuations and rhythmically-bedded pelagic carbonates of the Greenhorn Limestone (Upper Cretaceous). *4th North American Paleontological Convention. Abstracts with Programs*, Boulder, Col.: A48.

Winston, J.E. 1977. Distribution and ecology of estuarine ectoprocts: A critical review. *Chesapeake Science*, Solomons, Md., **18**: 34–57.

Wright, E.K. 1987. Stratification and paleocirculation of the Late Cretaceous Western Interior Seaway of North America. *Bulletin of the Geological Society of America*, New York, **99**: 480–490.